The Resilience of Marine Ecosystems to Climatic Disturbances

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The intensity and frequency of climate-driven disturbances are increasing in coastal marine ecosystems. Understanding the factors that enhance or inhibit ecosystem resilience to climatic disturbance is essential. We surveyed 97 experts in six major coastal biogenic ecosystem types to identify "bright spots" of resilience in the face of climate change. We also evaluated literature that was recommended by the experts that addresses the responses of habitat-forming species to climatic disturbance. Resilience was commonly reported in the expert surveys (80% of experts). Resilience was observed in all ecosystem types and at multiple locations worldwide. The experts and literature cited remaining biogenic habitat, recruitment/connectivity, physical setting, and management of local-scale stressors as most important for resilience. These findings suggest that coastal ecosystems may still hold great potential to persist in the face of climate change and that local- to regional-scale management can help buffer global climatic impacts.

Keywords: resistance, recovery, persistence, biogenic habitat, conservation and management

Human-induced climate change is affecting natural systems at an unprecedented rate (Lindner et al. 2010, Stocker et al. 2013, Barange et al. 2014). Even if greenhouse gases are stabilized at today's concentrations, climate change and its associated impacts will continue for centuries because of the inertia associated with ocean and climate processes (Field et al. 2014). Responding to climate-related risks in a changing world requires management strategies that support the capacity of ecosystems to cope with and adapt to climatic impacts (Hulme 2005, West et al. 2009, Field et al. 2014). Climate change therefore represents a new and fundamentally different problem for managers. One of the most significant contemporary challenges is to identify the factors that promote the resilience of natural systems (see box 1 for definitions) across a range of possible climate scenarios and other future anthropogenic changes (Hughes et al. 2005, Game et al. 2008, Ruckelshaus et al. 2013).

Coastal marine ecosystems in particular are under increasing pressure from climate-driven disturbances associated with ocean warming, acidification, sea-level rise, and the increasing frequency and intensity of storms (Hoegh-Guldberg and Bruno 2010). Many coastal ecosystems are built by foundational, habitat-forming species that are critical for supporting biodiversity, ecosystem functioning (Bruno and Bertness 2001), and a suite of critical ecosystem services (Barbier et al. 2014), but these species may be particularly vulnerable to climate-driven disturbance. Coral reefs, algal forests, seagrass meadows, oyster reefs, mangroves, and salt marshes build the three-dimensional structure that provides habitat for thousands of other species (Hoegh-Guldberg and Bruno 2010). Foundational species change physical conditions and can buffer environmental stress by attenuating waves during storm events. The loss of these structures consequently reduces marine habitat as well as the amount of natural wave protection at the coast (e.g., Gedan et al. 2011, Temmerman et al. 2013). Therefore, identifying the factors that sustain foundational species is crucial in maintaining ecosystem function and service provision under climate change and related escalating disturbances.

There are numerous and increasing records of climate-related declines in foundational species and their associated marine ecosystems (Alongi 2008, Waycott et al. 2009, Graham et al. 2015), but there are also instances in which these marine ecosystems have shown remarkable resilience against acute climatic events. For example, in Western Australia, up to 90% of live coral was lost in a severe bleaching event but recovered from a low of 9% to 44% of the reef

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Box 1. Definitions of ecological resilience. Definitions reported or cited in papers recommended by experts are marked with an asterisk (*).

Elton (1958): The possibility that communities are resistant to some perturbations and undergo no changes in structure on being perturbed.

Holling (1973)*: The measure of the persistence of systems and of their ability to absorb change and disturbance and still maintain the same relationships between populations or state variables.

Weston (1978)*: The degree, manner, and pace of restoration of the initial system function and structure following a disturbance.

Connell and Sousa (1983)*: A system can be considered stable in the face of a disturbance if (a) it retains a similar structure ("resistance") or (b) it returns to a similar predisturbance structure after an initial deviation ("resilience").

Pimm (1984): The ability of a system to resist disturbance and the rate at which it returns to equilibrium following disturbance.

Holling (1996), Gunderson (2000): The magnitude of disturbance that can be absorbed before the system changes its structure by changing the variable processes that control the behavior.

Folke and colleagues (2002): Resilience, for social–ecological systems, is related to the magnitude of shock that the system can absorb and remain within a given state, the degree to which the system is capable of self-organization, and the degree to which the system can build capacity for learning and adaptation.

Walker and colleagues (2004)*: The capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedback.

Desjardins and colleagues (2015): The capacity of a system to absorb change but maintain identity and a certain degree of integrity.

Operational definition used in this study: The persistence, throu gh either fast recovery or strong resistance, of the major habitat-forming taxa that define the structure of an ecosystem.

surface within 12 years (Gilmour et al. 2013). Similarly, kelp forests recovered within 5 years following 3 years of intense El Nino Southern Oscillation (ENSO)–related warming (Edwards 2004). These instances represent *bright spots*, demonstrating that there are conditions under which ecosystems persist even in the face of major climatic impacts.

Bright-spot analyses have typically been used in health fields to understand why some individuals or communities thrive whereas neighbors who are equally at risk do not. In these studies, bright spots are described as cases in which individuals or communities did better than normal (Sternin et al. 1997, Pretty et al. 2006). The concept can also be applied to ecological systems: By identifying instances of resilience in which ecosystems show high resistance or rapid recovery to climatic stress (box 1), we can uncover local conditions and processes that may allow ecosystems to maintain their structure and function and continue providing ecosystem services to humans. These insights can in turn guide conservation and management strategies for restoring the conditions that support resilience to climatic disturbance. For example, in an analysis of 2,500 coral reefs around the world, Cinner and colleagues (2016) identified 15 reefs that exhibited greater-than-expected fish biomass. These sites were characterized by factors (e.g., community-based management systems, strong reliance on reefs, and beneficial environmental conditions) that can be identified and promoted through management interventions.

Despite the importance of identifying the conditions that support nearshore ecosystem resilience to climate change, a synthesis of reported instances of bright spots from the literature is lacking. This is because comprehensively reviewing the literature on resilience of marine foundational species to climatic stress presents some formidable challenges. First, a single, agreed-on definition of resilience does not exist (box 1), and different studies have quantified responses in different ways. Second, terms such as *persistence*, *resistance*, *recovery*, and *resilience* are often used interchangeably, and *persistence*, *resistance*, and *recovery* are sometimes defined as components of *resilience* (e.g., Holling 1973, Connell and Sousa 1983, Pimm 1984; see also box 1). Moreover, the relative use of these terms has changed through time (figure 1, supplemental material). The frequency of the use of the term *resilience* has increased significantly over the past decades, with an average increase of 7.46% per year between 1984 and 2014 (figure 1; $R^2 = 0.57$, $F = 38.5$, $df = 29$, $p < .01$). *Resistance* and *recovery* decrease over time by –1.01% ($R^2 = 0.14$, $F = 4.6$, $df = 29$, $p = .04$) and –0.86% per year ($R^2 = 0.15$, $F = 5.05$, $df = 29$, $p = .03$), respectively. A final challenge is that papers mentioning resilience often report the lack of resilience rather than a demonstration of resilience (e.g., Fraser et al. 2014, Koch et al. 2014). For example, the top 10 most-cited papers referring to the resilience of marine ecosystems faced with climatic changes all emphasize negative impacts (supplemental table S1). Although the literature shows negative change or impacts in coastal marine ecosystems around the globe (e.g., more than 75% of coral reefs, more than 85% of oyster reefs, and more than 60% of salt marshes are severely depleted; Pandolfi et al. 2003, Beck

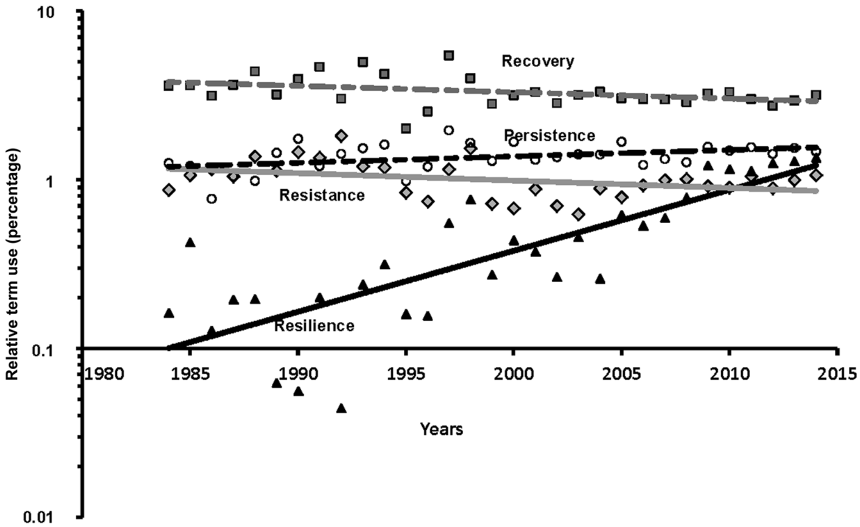

Figure 1. Temporal trends in the relative use of the terms **recovery** *(the grey filled squares),* **persistence** *(the empty circles),* **resistance** *(the grey filled diamonds), and* **resilience** *(the black filled triangles) in peer-reviewed publications on marine ecosystems subject to environmental shocks and natural and anthropogenic disturbance (see the supplemental materials for details). Regression lines are included for each term.*

et al. 2011, Lotze 2006), the remaining areas may contain unreported locations where ecosystems are resilient to climatic stress and disturbance.

Taken together, the above points call for a need to summarize the available knowledge to better inform management and to identify areas where more research is needed. Here, we used expert knowledge elicitation as a first step toward identifying bright spots of resilience in coastal biogenic ecosystems and understanding their key underlying processes. We define *bright spots* as places where biogenic habitat is maintained following climatic disturbance rather than a quantitative assessment of the drivers of ecosystem condition (e.g., Cinner et al. 2016).

Expert elicitation is widely used as a cost-effective method to produce estimates in a variety of disciplines in which there is extensive expert knowledge but little published data for some aspects of interest (e.g., Martin et al. 2005, Halpern et al. 2007). To uncover and synthesize expert knowledge on the presence of resilience bright spots, we developed an online survey that we sent to experts in each of six key marine coastal biogenic ecosystem types: coral reefs, kelp forests, mangroves, oyster beds, seagrass beds, and salt marshes. We asked the following three questions: (1) Are there examples of resilience to climatic disturbances in each ecosystem type? (2) Under what contexts did resilience occur? (3) What factors did experts consider most important in promoting or preventing resilience to climate change, based on their career knowledge? We augmented the expert survey by reviewing articles (n = 129) suggested by the experts in the survey as the most important publications relevant to resilience to climatic impacts in each ecosystem type. The review of recommended articles allowed us to assess whether expert opinions are borne out in key literature. On the basis of this information, we identify the key factors shown to promote or prevent resilience and discuss these in a management context.

Expert survey

We surveyed experts working in six major coastal biogenic ecosystems to identify occurrences of resilience, examine the context in which resilience occurred, and understand factors that contribute to or prevent resilience across ecosystems in the face of climatic disturbances. A majority of definitions of resilience (8 of 10; box 1) include the maintenance of ecosystem structure, state, function, or identity in the face of disturbance. We used this concept as a starting point to develop an operational definition of resilience as "persistence, through either fast recovery or strong resistance, of the major habitat-forming taxa that define the structure of an ecosystem." Therefore, if habitat-forming taxa persisted, we considered the system resilient, even if the species composition of the habitat-forming taxa or associated taxa has changed (e.g., branching corals being replaced by massive corals). We recognize that this definition does not address ecosystem function or the feedbacks that maintain it; however, we needed a definition that was simple and broad enough to capture the knowledge of researchers using diverse methods across diverse systems. We defined climatic disturbances as either chronic (e.g., ocean acidification, increasing temperature, and sea-level rise) or acute events (e.g., extreme storms, ENSO events, heat waves, and floods).

We created the survey (figure 2) using the online tool SurveyMonkey (*www.surveymonkey.com*). A link to the survey was emailed individually to each expert on 27 February 2014, and the experts were given 2 months to respond. *Experts* were identified as the top 50 authors (by number of papers published) in each of six ecosystem types in Web of Knowledge, generating a list of 300 experts (using scientific productivity as an indicator of expertise). We included experts on ecosystems rather than resilience experts, because we sought to broadly determine the prevalence of resilience following climatic disturbance. Had we limited our responses to only experts on resilience, we would have had a much smaller group to elicit information from, covering a narrower geographic area. The type of horizon scanning we used (polling experts who were identified on the basis of their productivity) has similarly been used in other expert judgment elicitation studies (e.g., Sutherland et al. 2013).

The survey comprised 13 questions that addressed three goals: (1) identify specific examples (henceforth *expert*

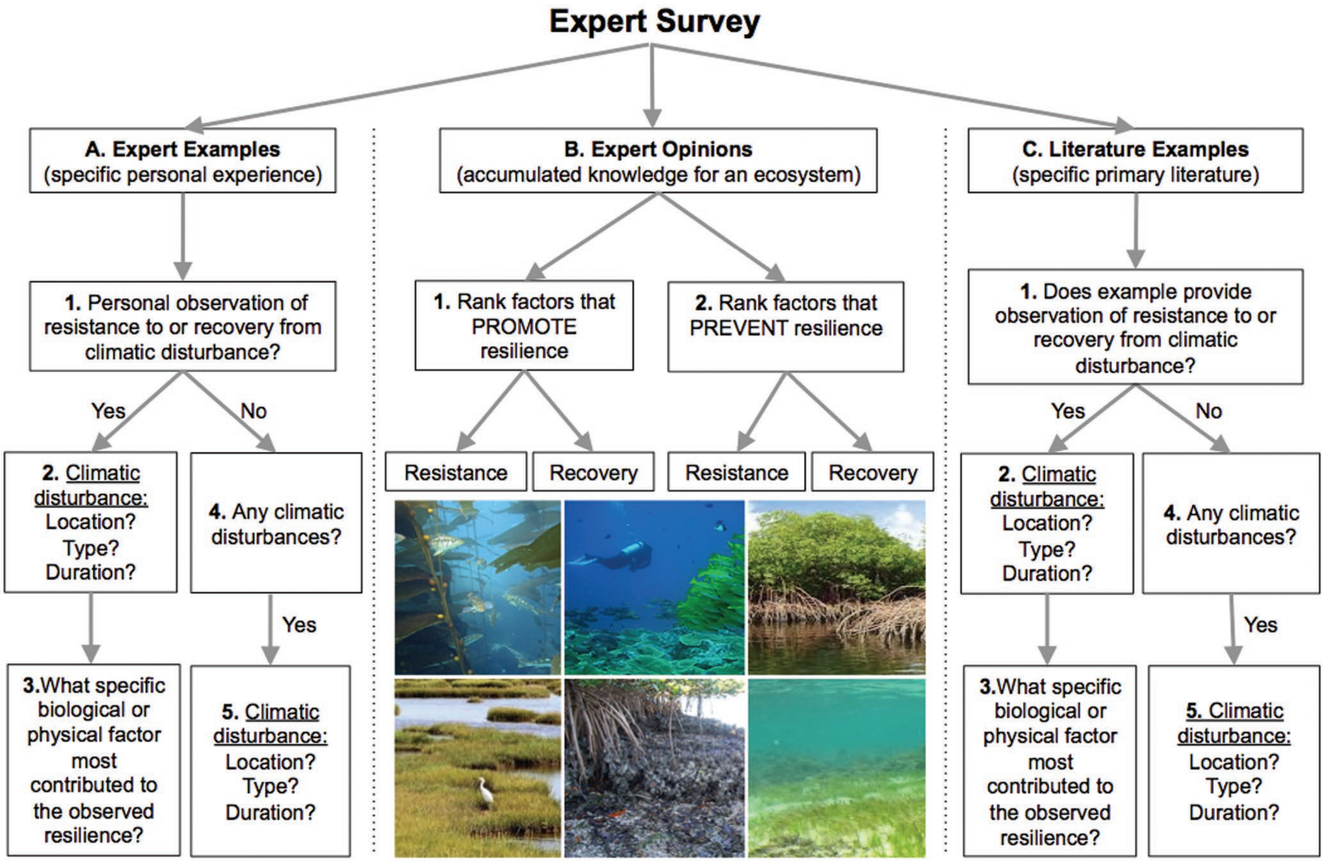

Figure 2. A schematic outline of the questions asked in the online expert survey. The respondents were asked to provide examples of observed resilience to climatic impacts from their own research experience (a), to rank the importance of factors promoting or preventing resilience (b), and to indicate relevant peer-reviewed papers addressing resilience in coastal biogenic ecosystems (c). The photographs present examples of each ecosystem type: kelp forests, coral reefs, mangrove forests (top row, left to right), salt marshes, oyster reefs, and seagrass beds (bottom row, left to right).

examples) of ecosystem resilience, or lack thereof, to climatic disturbances and the context in which these examples occurred; (2) accumulate knowledge of possible factors and processes supporting or preventing resilience on the basis of experts' perceptions or opinions (henceforth *expert opinions*); and (3) collect experts' recommendations of key papers (henceforth *expert-recommended literature*) addressing this topic (figure 2, supplemental table S2). We asked the respondents to focus their answers on the ecosystem type in which they were considered an expert. Additional questions were included to define the ecological and geographic scope of the respondents' expertise. Responses to questions were multiple choice (check boxes) or open ended (the respondents typed in text). The three types of information collected in the survey (expert examples, expert opinions, and expert-recommended literature) were then summarized (as we describe below), and the results were compared to determine the frequency with which resilience is encountered and the factors that contribute to or prevent resilience.

Expert examples. To evaluate accounts of resilience to climatic disturbance from published as well as unpublished or unreported cases, we asked the experts whether they had personally encountered instances of resilience ("Expert Examples"; figure 2a). We determined the proportion of the experts who had witnessed evidence of resilience, excluding responses of the experts who reported resilience unrelated to climatic disturbance (e.g., nutrient additions or disease outbreaks) and the experts who had never witnessed disturbance events. To test for a possible influence of the length of the respondents' experience in a particular ecosystem type, we used a logistic regression to test whether the observations of resilience for each respondent (1, *yes*; 0, *no*) were related to the length of their experience in the ecosystem or to the ecosystem type. For each instance of resilience, we asked the experts to report the type and length of climatic disturbance along with what factors they felt contributed to resilience (in their own words). We classified these factors into one of eight factor groups (table 1a–1b) that were preselected from a preliminary examination of the 10 most commonly cited papers in each ecosystem. An additional group, "other," was used for factors that did not fit into the eight categories; the experts were asked to type in what the "other" factor was. If the experts had not encountered

Table 1a. Factors promoting the resistance or recovery of coastal biogenic ecosystems included in the expert survey.

Survey response option	Description and examples
Adequate recruitment or connectivity	Supply of new recruits and connectivity with adjacent sites via larval or propagule dispersal (e.g., Thrush et al. 2013)
High levels of beneficial species interactions	Intact trophic structure facilitating key processes such as herbivory and predation or mutualisms can help maintain biogenic habitat and increase resistance to climatic stressors (e.g., Mumby et al. 2007)
Physical setting	Favorable temperature, currents, isolation, or position relative to sediment source can provide increased resistance to climatic stressors by ameliorating their effects (e.g., Alongi 2008)
Adequate remaining biogenic habitat	High amount of biogenic habitat maintained after disturbance (e.g., Guzman and Cortés 2007)
Genetic diversity or adaptation	Amount of existing genetic diversity prior to a disturbance that enables some proportion of biogenic habitat to survive disturbance (e.g., Hughes and Stachowicz 2004)
Functional diversity or redundancy	Multiple species that play similar roles in an ecosystem prevent system collapse if some species are lost (e.g., Palumbi et al. 2008)
Remoteness or low human accessibility	Level of isolation from any human disturbance (e.g., Gilmour et al. 2013)
Conservation and management measures	Active management to preserve an ecosystem or reduce nonclimatic forms of stress (e.g., fisheries restrictions or marine protected areas; Micheli et al. 2012)

Table 1b. Factors decreasing the resistance or preventing the recovery of coastal biogenic ecosystems included in the expert survey.

Survey response option	Description and examples
Space preemption preventing recovery	Phase shifts to alternative stable states caused by disturbance that then prevent recovery of the original habitat-forming species (e.g., Perkol-Finkel and Airoldi 2010)
Additional chronic (biotic) disturbance	Disease, invasive species, predator, or grazer outbreaks that reduce the ability of a system to withstand climatic stress (e.g., Hughes et al. 2003)
Additional local anthropogenic stressors	Local harvesting, nutrient input, or other localized human disturbance that reduces the resilience of systems to climate disturbance (e.g., Strain et al. 2015)
Additional global climatic stressors	Global stressors (such as ocean acidification) that reduce ecosystem resilience (e.g., Hoegh-Guldberg et al. 2007)
Lack of adequate management	Inadequate protection of ecosystems or habitats leading to reduced resilience (e.g., Beck et al. 2011)

instances of resilience, we asked for the type and length of climatic disturbance(s) witnessed in their study sites, if any. To understand the context under which resilience occurred, we compared the proportion of cases with resilience by disturbance length (ranging from hours or days to more than 100 years or ongoing) and type. The disturbance types were grouped into five categories: increased temperature, storms, ENSO events (storms and increased temperature), inundation and other hydrodynamic changes, and multiple climatic stressors. Finally, to determine the frequency with which factors promoting or preventing resilience were reported, we calculated the number of times a specific factor was mentioned in each habitat divided by the total number of mentions for all factors in that habitat. Although some of the experts listed two factors that promoted or prevented resilience, these were treated as individual observations when calculating factor frequencies. We then averaged the results across habitats.

Expert opinions. On the basis of their general knowledge of their focal ecosystem, the respondents were then asked to rank eight factors in terms of their perceived importance in contributing to resilience, as well as five factors in their perceived importance in preventing resilience ("Expert Opinions"; figure 2b). We selected these factors through a preliminary literature review of the 10 most-cited papers for each ecosystem (table 1). For each factor, the rankings were the following: *very important*, *somewhat important*, *not important*, *unsure* (i.e., "I don't know the answer"), or *unclear* (i.e., "I don't understand the question"). The rankings were done separately by habitat type and then averaged for each of the two components of resilience: resistance and recovery. In addition, the experts were given the option of listing and ranking additional factors not specified in the questionnaire. We compared the factors ranked as very important with the factors that were cited in expert examples and in the expert-recommended literature (see section below).

Expert-recommended literature. We asked the experts to list the top one to three papers that in their opinion offered the best examples of literature on resilience in their focal ecosystem. This provided us with expert-recommended literature on resilience by ecosystem type (figure 2c). Of the 129 recommended papers, 76 were not relevant to our study because: the paper did not include a natural climatic disturbance and ecosystem response ($n = 46$), it was not focused on habitat-forming species ($n = 14$), the paper was about restoration rather than resilience ($n = 9$), it was a general review or monitoring guide without specific examples ($n = 5$), the study ended at the disturbance ($n = 1$), or the paper could not be

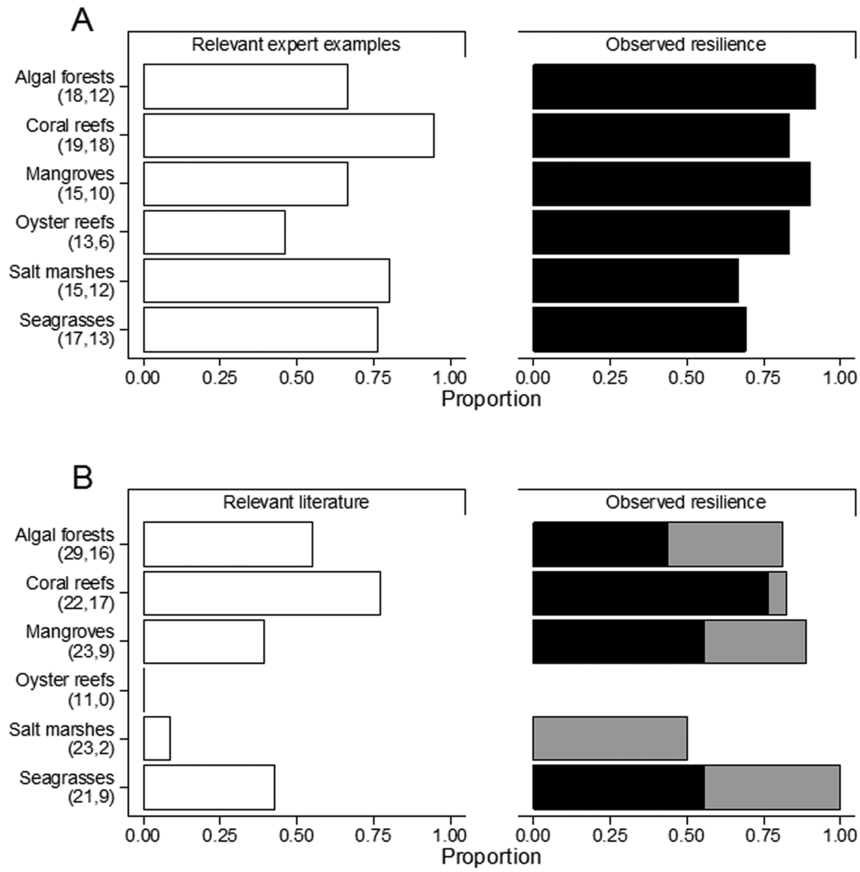

Figure 3. The prevalence of resilience in expert examples and expert-recommended literature. (a) The proportion of the respondents, by ecosystem type, who reported at least one instance of climatic disturbance during their career (white bars) and the proportion of these experts who had witnessed resilience (either resistance or recovery) following climatic disturbance (black bars). (b) The proportion of papers recommended by experts that focused on field observations of at least one climatic disturbance, included information on habitat-forming species, and included observations after the disturbance (white bars) and the proportion of these relevant papers that found either resilience (black bars) or context-dependent resilience (grey bars). The sample sizes are given in the y-axis, with the first number representing the total number of expert respondents or recommended papers and the second number indicating the number of relevant cases.

found with the information provided (n = 1; supplemental table S3). We discarded these articles and focused on the 53 papers relevant to resilience following a natural climatic disturbance. For the relevant papers, we evaluated the proportion of cases with resilience. To determine the context in which resilience occurred, we also assessed resilience by disturbance type (in the five categories described above) and disturbance length. Finally, as for expert examples, we evaluated the factors reported to promote or prevent resilience using the factor categories listed in table 1. For each habitat, we calculated the number of times a specific factor was mentioned and divided by the total number of mentions for all factors (by habitat), using separate calculations for factors promoting and preventing resilience. We then averaged results across habitats. Only two of the relevant papers focused on salt marshes, so this habitat is underrepresented in this data set, and oyster reefs are not included here because no recommended papers on this habitat met our criteria.

Occurrence and context of resilience

A total of 97 experts (a 32.3% response rate) completed the online survey, with 13–19 responses for each ecosystem type (supplemental table S4). The research experience of the respondents in their focal ecosystem ranged between 5 and 60 years (mean = 25.4 years, standard deviation = 9.6, median = 25 years; table S4). The experts' research experience spanned global locations, although the United States, Europe, and Australia had the highest representation (supplemental figure S1a).

Over two-thirds of the 97 experts (69%, n = 67) reported observations of resilience during their career. However, a quarter of the experts did not observe climatic disturbances (n = 26). Excluding these cases, 80% of experts had witnessed resilience following climatic disturbance. Expert examples of resilience were reported for each of the six ecosystem types, with resilience to climatic disturbance ranging from 67% for salt marshes to 92% in algal forests figure 3a, supplemental table S5). The probability of observing resilience was not significantly related to the respondents' experience (p = .73) or ecosystem type (p = .53). There was a marginally significant interaction between years of experience and ecosystem (p = .054; supplemental figure S2), but this effect should be interpreted with caution given there were few instances of no observed resilience. Expert examples of resilience originate mainly from the United States, Australia, and Europe, reflecting the distribution of experts (60% of cases; figures S1a–S1b), although over one-third of the examples of resilience were also found in various other geographic locations (figure S1b).

Similar to expert examples, resilience was found in relevant expert-recommended papers across all ecosystem types in 85% of the papers (45 of the 53 relevant papers; figure 3b). Among these, 28% of the relevant papers (15 papers) demonstrated context-dependent resilience, in which resilience was found in some conditions but not others. Only six of the

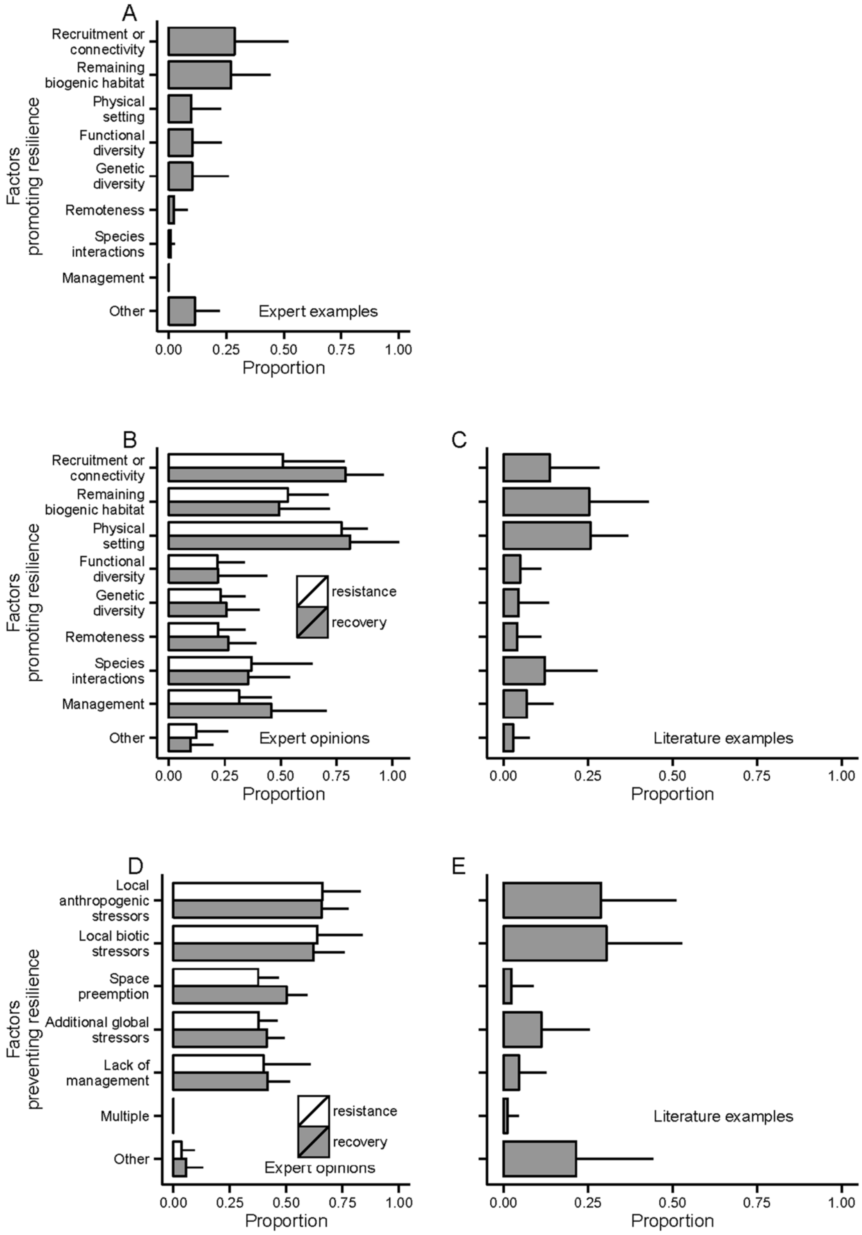

Figure 4. The factors promoting resilience (a–c) and preventing resilience (d–e) according to expert examples (a), expert opinions (b, d), and literature suggested by experts (c, e). In (a), we present the proportion of times the experts listed a *factors as promoting resilience, with a total of 73 factors mentioned by the 57 experts that had witnessed resilience following climatic disturbance. In (b), we present the proportion of experts who listed each of the categories as "very important" in promoting resilience (*n *= 97 experts). In (c), we present the proportion of times recommended papers listed* a *factors as promoting resilience, with a total of 74 factors highlighted in 53 relevant papers. In (d), we present the proportion of experts who listed each of the categories as "very important" in preventing resilience (*n *= 97 experts). In (e), we present the proportion of times recommended papers listed* a *factors as preventing resilience, with a total of 60 factors highlighted in 53 relevant papers. In (e), we included the factor "multiple" when there were more than two factors reported as equally affecting resilience. In all panels, we present mean proportions (+ 95% confidence intervals), averaged across ecosystem types. Therefore, the error bars can be interpreted as a measure of consistency between ecosystem types.*

relevant expert-recommended papers included definitions of resilience (see box 1). There were only a few cases in which multiple experts recommended the same paper: 1 paper (Gilmour et al. 2013) was recommended by six experts in coral reef ecosystems, and 15 papers were recommended by two to three experts (table S3). Therefore, 87% of papers were mentioned by only 1 of the 97 respondents.

The most commonly reported climatic disturbances in both expert examples and expert-recommended literature were storms (40% and 30% respectively). Resilience was observed across all disturbance types, varying between 73% and 86% in expert examples (supplemental figure S3a, supplemental table S6a) and between 31% and 94% in the relevant expert-recommended literature (considering both resilience and context-dependent resilience; supplemental figure S3b, supplemental table S6b). Considering both expert examples and expert-recommended literature, the length of disturbance varied from hours to more than 100 years or ongoing, and resilience was found across all disturbance lengths (supplemental figure S5a–S5b). For expert examples, the majority (45%) of disturbances lasted between hours and months, whereas for expert-recommended literature, the majority of cases were ongoing disturbances (21%) and multiple lengths of disturbance (25%), likely because a number of papers were reviews with several examples or spanning longer time periods.

Factors promoting and preventing resilience. Remaining biogenic habitat and recruitment/connectivity were the most frequently cited factors promoting resilience when considering all sources of information: expert examples, expert opinion, and expert-recommended literature (figure 4)—although physical setting and management were also cited very frequently in expert opinion and expert-recommended literature (figure 4b–4c).

There was little difference in factors ranked by experts as important for promoting resistance versus recovery, except that recruitment/connectivity and management were more commonly ranked as strongly important for recovery than resistance (figure 4b). There was also little difference in factors ranked as important across ecosystems (figure S5a–S5b), except that physical setting was not as commonly ranked as very important for recovery in coral reef systems compared with that in the other ecosystems.

When evaluating factors that may prevent resilience, the experts ranked all five provided factors (table 1) relatively highly, although local factors (i.e., additional local biotic disturbance and local anthropogenic stress) were most commonly considered very important in expert opinions (63% and 66%, respectively, for resistance and recovery; figure 4d) and in expert- recommended literature (30% and 31%, respectively, for resistance and recovery; figure 4e). There was little difference in rankings between factors preventing resistance versus preventing recovery other than for space preemption, which was more commonly a factor in recovery (figure 4d). The factors ranked by the experts as very important were similar across the six ecosystem types (supplemental figure S5c–S5d), except that additional chronic biotic disturbance and lack of adequate management were more commonly viewed as very important among oyster-reef experts. For factors promoting and preventing resilience, there were only a few novel "other" responses written in by experts that were not included in our survey (notably, limited growth or inadequate research for factors preventing resilience).

For each factor listed in the survey of expert opinion, we gave the experts the option to indicate whether they were unsure about the importance of a particular factor. For factors promoting resilience, more experts reported being unsure about genetic diversity (31%) compared with other factors (3%–17%; supplemental figure S6a). For factors preventing resilience, the role of additional global climate stressors and space preemption had the highest percentage of the experts being unsure (12% and 10%, respectively), although relatively fewer experts indicated uncertainty across all factors (supplemental figure S6b) compared with uncertainty regarding factors promoting resilience.

Discussion

By surveying experts, we were able to access decades of experience on climatic stress and the response of biogenic habitats and elicit data that have been scarcely reported in the literature. Our survey indicates that bright spots of ecosystem resilience are surprisingly common across six major coastal marine ecosystems: 80% of the experts and 87% of the relevant recommended papers reported instances of resilience to climatic disturbances. In both expert examples and expert-recommended literature, resilience was found across a wide range of climatic disturbance types and lengths, indicating that ecosystems can be resilient to even long-term chronic climatic stress. These bright spots represent opportunities for identifying and evaluating factors that support the resilience of coastal ecosystems undergoing climatic stress, thereby providing important information for the conservation and management of current and likely future conditions. The frequency with which we encountered instances of resilience in the expert examples and recommended literature does not contradict the overwhelming evidence that climatic impacts present a major stressor to coastal ecosystems. Instead, it provides optimism that we can indeed identify and manage for conditions that facilitate resilience to climatic stress.

Although a suite of factors were deemed important in promoting resilience to climatic impacts, recruitment/connectivity and remaining biogenic habitat were ranked most commonly as very important across expert examples, expert opinion, and expert-recommended literature. In addition, physical setting and management were ranked highly in the expert opinion and recommended literature. This indicates that the protection of habitat and populations at locations where conditions may promote resilience can maintain sources of regrowth and replenishment and may be the most effective approach to supporting coastal resilience in the face of increasing threats from climate change. The high frequency with which local stressors (both anthropogenic and biotic) were cited as important in preventing resilience in both the expert opinion and expert-recommended literature further supports the role of local conservation and management in increasing resilience. Below, we discuss the factors ranked by the experts as very important, with specific examples from the focal ecosystems and management strategies for enhancing resilience to climatic impacts.

Factors promoting resilience. High levels of recruitment or connectivity were commonly cited in expert examples and recommended literature as leading to rapid recovery following disturbances, especially in algal forests and coral reefs but also in examples from mangroves, oyster reefs, and seagrass beds. In the most commonly recommended paper, Gilmour and colleagues (2013), an isolated reef in Western Australia recovered from a mass bleaching event (1997–1998 ENSO) within 12 years because of self-replenishment through larval recruitment. Similarly, coral reefs affected by the 1997–1998 ENSO warming event in the Chagos Archipelago recovered within 8 years (although in juvenile form lacking complex structure) because of recruitment (Sheppard et al. 2008). In algal forests, the presence of a seed bank, the abundance of zoospores, and the fast growth rate of algal species were cited as reasons for recovery following climatic disturbance. For example, the recovery of giant kelp (*Macrocystis pyrifera*) from deforestation caused by ENSO events and storms was due to high recruitment (Dayton et al. 1992, Edwards 2004), although the rate of recovery was variable across the range (within 6 months in California, United States, and up to 2 years in Baja California, Mexico) because of local biotic and abiotic factors (Edwards 2004). In mangroves, Alongi (2008) reported considerable resilience to sea-level change over historical time scales globally and attributed this resilience to continuous propagule production, long propagule duration, and wide dispersal. In oyster reefs, adequate recruitment has driven the recovery of abundance along the Gulf of Mexico, United States, following storms because of an extended spawning season (Pollack et al. 2011, cited by Munroe et al. 2013). In seagrass meadows, there has been a general debate in the literature regarding the role of recruitment versus clonal growth for recovery following disturbance, with most cases of recovery from clonal growth rather than from recruitment, because few recruits survive (Walker et al. 2006). However, large-scale increases in seagrass cover over several decades have occurred where the recruitment of seedlings played a key role in colonization and recovery, although recovery was following nonclimatic disturbance (Kendrick et al. 2000).

From the expert examples, remaining biogenic habitat was the most common factor cited for promoting resilience. The examples indicate the diverse roles that remaining habitat played in enhancing resilience. These included the persistence of gametophyte stages in kelps and seedlings in seagrasses; recruitment from surviving individuals in algal forests and coral reefs; the regenerative capacity of toppled corals following storms; clonal revegetation in seagrass meadows from surviving individuals; the survival of mangrove seedlings, allowing the rapid regeneration of forests; and remaining structure influencing local hydrodynamics to improve growth rates among surviving corals or to increase sediment retention in mangroves. Similar aspects of remaining biogenic habitat were reported in the recommended literature. For example, in salt marshes in the southeastern United States, the recovery of marsh plants following drought (a climatic hydrodynamic change) occurred in areas adjacent to remaining healthy marsh, although only where fronts of grazing snails were absent (Silliman et al. 2005). Similarly, in Gilmour and colleagues (2013), high growth rates of remnant coral colonies contributed to the rapid recovery of coral cover after bleaching by allowing for later self-replenishment through recruitment. Although there was no recommended literature for oyster reefs that met our criteria, there were examples of remaining biogenic habitat leading to recovery following nonclimatic disturbance whereby the rapid growth of remaining small individual oysters allowed recovery of oyster beds in Delaware, United States (Munroe et al. 2013).

Physical setting surfaced in expert examples related to hydrodynamics and upwelling, proximity to sediment sources, and depth. Similarly, in expert-recommended literature, hydrodynamics and upwelling, depth, and location within bays and estuaries (elevation and salinity influences) were commonly cited. For example, in seagrass meadows, depth was a predictor of recovery because of the influence of light on growth (Marbà and Duarte 2010). Physical setting was also important in alleviating some of the stress associated with the disturbance. For example, locally turbid sites had lower incidences of coral bleaching (Bayraktarov et al. 2013). Local physical setting was a factor in maintaining sediment delivery in salt marshes (Day et al. 2011) and in mangrove forests (Gilman et al. 2008). In some cases, physical setting was linked to resilience because of proximity to rivers, which can affect water quality after storms. In Florida, for example, seagrasses farther from river mouths had higher resilience because river outflow altered salinity, turbidity, and phytoplankton blooms following hurricanes, and these impacts were more severe than the initial physical loss (Carlson et al. 2010). Although referring to bright spots in the context of the maintenance of fish biomass rather than biogenic habitat, a recent paper also found that bright spots were associated with particular physical settings (along with several social parameters; Cinner et al. 2016).

Factors preventing resilience. The experts most commonly ranked local anthropogenic and biotic stressors as very important in preventing resilience to climatic impacts. These factors also were commonly indicated as preventing resilience in expert examples and recommended literature. For example, mangrove resistance to sea-level rise can be decreased by human activities within the mangrove catchment (e.g., the development of impervious surfaces and groundwater extraction) that alter sediment supply (Gilman et al. 2008). In coral reefs, examples of rapid recovery at remote locations suggest that extremely high rates of growth and recruitment are possible in reefs isolated from human influence (e.g., Sheppard et al. 2008, Gilmour et al. 2013). However, even in the populated islands of the Seychelles, where a major bleaching event resulted in loss of more than 90% of coral cover, over half of the reefs recovered to predisturbance levels within 15 years (Graham et al. 2015). Reefs that recovered were structurally complex, had high density of juvenile corals and herbivorous fishes, and had low nutrient loads (Graham et al. 2015)—all factors that can be enhanced by local to regional level management. The reduction of local stressors has been shown to enhance resilience to climatic factors in other biogenic habitats as well: Decreased nutrient loadings to algal forests (Fucoids) have increased the survival of recruits despite high wave exposure and have increased survival and growth of juveniles despite high temperature (Strain et al. 2015). In salt marshes, Silliman and colleagues (2005) provided an example of local biotic forces mediating recovery: Overgrazing by snail fronts synergistically increased the susceptibility of marsh plants to drought. Although not explicitly addressed by Silliman (2005), numerous authors have called for the management of top predators and herbivores in order to keep trophic dynamics intact and increase the resilience of biogenic habitats, including kelp forests (Estes et al. 1998, Steneck et al. 2002) and coral reefs (e.g., Birkeland et al. 1982, Mumby et al. 2006).

Implications for management. There are existing conservation strategies that can be effective for managing the factors highlighted as critical in promoting or preventing resilience. These strategies were developed to promote resilience generally, but on the basis of our results, these should be equally important in promoting climatic resilience. Protecting source populations will help maintain the remaining biogenic habitat needed for promoting recruitment of foundation species and connectivity between populations. This can be achieved via marine protected areas (MPAs) that are spaced appropriately given the reproductive output and dispersal potential of a given species (e.g., Gaines et al. 2010, De Leo and Micheli 2015). Protection of large, fecund individuals in MPAs can also maintain the reproductive and recruitment potential of populations depleted by climate-driven mass mortalities (Micheli et al. 2012). In addition, fisheries management that maintains trophic structure can enhance the resilience of foundation species (Steneck et al. 2002, Hughes et al. 2003). For example, in some coral reef ecosystems, the reduction of predatory fishes has led to the overpopulation of reefs by sea urchins, which both directly erode corals and indirectly affect recruitment by reducing the crustose algae that is critical settlement habitat (O'Leary and McClanahan 2010, O'Leary et al. 2012). Similarly, the removal of top predators can induce trophic cascades, leading to the loss of foundation species in kelp forest ecosystems (Estes et al. 1998). Therefore, the protection of predators and trophic interactions can enhance both remaining biogenic habitat and recruitment.

Protecting remaining biogenic habitat and enhancing recruitment can also be achieved when functional redundancy and genetic diversity are protected. Management to increase functional redundancy in the form of diverse foundational and consumer species can help the system persist despite the loss of any one species (Micheli and Halpern 2005, Palumbi et al. 2008). Genetic diversity has been shown to enhance the resistance of seagrass meadows to grazers, which can increase resilience to climatic stress (Hughes and Stachowicz 2004). Similarly, genetic diversity is related to higher production of flowering shoots, increased seed germination, and increased leaf shoots (Williams 2001)—all of which enhance recruitment and clonal reproduction. Protection of the most resilient ecosystems (and the foundation species that generate them) could also lead to significant co-benefits, because resilient ecosystems can in turn ameliorate environmental stress, mitigate climate-related risks, and be major players in carbon storage while waiting for global emission reductions (Duarte et al. 2013, Ferrario et al. 2014).

Although physical setting may be outside the control of local management, it can be considered in marine spatial planning and in the siting of MPAs. By determining what settings and conditions provide the greatest resilience in the face of climate change and protecting these from human disturbance, managers may enhance the ability of ecosystems to withstand climatic disturbances. Numerous experts and papers indicated that local hydrodynamics can play a key role in resilience and that these factors should be considered along with ecological system characteristics in the placement of MPAs (Gaines et al. 2010).

Conclusions

The results of this survey highlight key factors we can manage, but they also reveal the need to direct research toward better understanding the contribution of factors that are still poorly understood. The experts were most uncertain about how genetic and functional diversity contribute to ecosystem resilience. However, these factors may be strongly linked to the maintenance of biogenic habitat (e.g., Hughes and Stachowicz 2004, Ehlers et al. 2008). In addition, we need to better understand where management fits within the context of resilience and how science can contribute to management. Conservation and management measures were not frequently mentioned in the expert examples as being very important in promoting resilience, although they were frequently cited in the expert opinion and the expert-recommended literature. However, the highest-ranked factors for promoting resilience can be managed, and the factors considered important in preventing resilience were local stressors that can also be addressed through management. The experts therefore recognize that the effects of conservation and management measures may play an important role in promoting resilience, but in their personal experience, management has not played as large a role. This disconnect may reflect the focus of the survey participants (researchers rather than managers) or may reflect the general gap between science and management (Carpenter and Folke 2006, Knight et al. 2008). Proposed conservation strategies and available monitoring data often fail to lead to management action. This can occur because of differences in research and management scales of interest, because managers lack access to scientific data or publications, or because there is no framework within management systems that helps managers incorporate scientific data into decision-making. Therefore, there is an ongoing need for enhanced collaboration and communication between scientists and managers, capacity building, and the development of management frameworks that help managers and stakeholders identify management-targeted research needs (Parma 1998, Carpenter and Folke 2006). Finally, expert surveys such as the one used here can help collate years of experience and identify management approaches that have been successful. Carrying out similar surveys with managers would provide further information about what works on the ground and build on the experiences shared here by researchers.

The escalating impacts of climatic change on marine ecosystems and ecosystem services require that the conditions and processes enabling resilience are understood and supported. It is important to identify bright spots of resilience to climate disturbance and the circumstances that promote them in order to foster the conservation of marine ecosystems and their associated services. The observation of resilience in more than 80% of the expert responses provides a much-needed note of ocean optimism: Some nearshore marine ecosystems have the necessary characteristics and conditions to resist and recover from current climatic impacts. Furthermore, our results indicate that two existing conservation and management strategies, the reduction of additional local stressors and the use of marine spatial planning, may be the most effective approaches to promoting resilience. Reducing the cumulative impacts to biogenic ecosystems during climatic disturbance is essential for maintaining at least some biogenic structure and source populations that can provide for post-disturbance recruitment and regrowth. Careful spatial planning of marine activities, including the appropriate placement of MPAs, can maintain adequate recruitment and biogenic habitat complexity and leverage the influence of physical setting in supporting resilience. The existence of local and regional tools that managers already have experience applying should aid in the ability of ecosystems to cope with climatic disturbance, while society strives to reduce global emissions and reduce global climatic threats. Additional tools are likely to emerge as managers and researchers gain experience managing for resilience to climatic impacts. Therefore, our results indicate that although marine ecosystems face growing cumulative stress from coupled human perturbations and climatic instabilities, they still harbor enormous capability for resilience. Maintaining and rebuilding this capacity should be a major focus of marine science and management.

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Supplemental material

Supplementary data are available at *BIOSCI* online.

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